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# A Contribution to the Embryology and Phylogeny of the Pycnogonids.

Thesis

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by

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## A Preliminary Note on the Embryology of the Pycnogonids. By T. H. Morgan.

The position of the Sea Spiders, amongst the Articulates, and the speculations as to the relationship of this to other orders, have been almost entirely based on the anatomy of the adult animal. Kröyer, in 1840, described some embryos, and Dohrn and Hoek have carried this a step further. Owing to the extreme difficulties of technique, nothing is known of the internal changes that take place during development.

A study of the germ layers and their subsequent differentiation into organs ought to throw, I thought, some light on the phylogeny of these most interesting animals. Material for work was collected during the summer of 1889 at Wood's Holl, Mass., and I am under very great obligations to Professor McDonald for the opportunity to collect and study at the laboratory of the Fish Commission Station.

Three species of Pycnogonids are found amongst the sea-weeds and hydroids about Wood's Holl, viz.: Phoxichilidium maxillare, Tanystylum orbiculare, and Pallene empusa. During July and August these carry eggs. The first two genera have a small free-swimming, six-legged larval stage. In Pallene the eggs are much larger, resulting in abbreviated development, and the young leave the cluster of eggs, carried by the male, in a practically adult condition.

In Phoxichilidium and Tanystylum the egg undergoes a regular segmentation into 2, 4, 8, 16; all the segments being equal. After one or two more divisions a condition is reached as shown by Fig. 6. Here the segments have the form of pyramids, with the apices together at the centre of the egg. A nucleus is at the outer part of each pyramid. The egg continues to divide, the pyramids becoming smaller, and then each pyramid divides into an outer and an inner part, each part with a single nucleus. See Fig. 7. Here we have a most perfect delamination, resulting in an outer circle of ectodermal cells and an inner mass of cells. Both inner and outer cells continue to divide. Many of the inner cells now break down, as is seen in the endoderm of many Coelenterate planulae, and the cells of the outer circle become smaller; the line of demarcation between inner and outer cells remains sharp and distinct. It is very difficult to follow out the fate of these two cell masses. Many of the inner cells seem to form a yolk-like substance, with a few scattered nuclei, while the outer cells form undoubtedly the ectoderm of the adult. I believe the endoderm to be formed from some of the nuclei of the inner cells, but I cannot be entirely certain of this, nor have I any observations as to the origin of the mesoderm.

In Pallene, on account of the much larger and more manageable eggs, I have been able to carry out in much more detail the origin and fate of the germ layers. The eggs measure .25 mm. in diameter, and have 125 times the volume of the preceding species. The segmentation is quite interesting, and I had the good fortune to be able to follow it quite far along in the living egg.

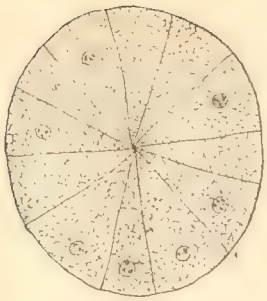

Fig. 6.

Fig. 7.

The first furrow divides the egg into two very unequal parts—a large macromere and a small micromere. The latter is about one-fourth the size of the first. Each segment has a single nucleus. The next furrow—at right angles to last—divides each of the first two into two equal halves. In some cases the larger cell divided five minutes before the smaller, but in other cases the reverse process took place. The furrows dividing the egg into these four parts *nearly* coincide for the micromeres and macromeres. The third furrow divides both micromeres and macromeres into four each, and is at right angles to the first two planes of division. The next furrow is seen to divide the four macromeres into eight, is at right angles to the last two furrows, or is parallel to the first plane of segmentation. At the same time each micromere divides into two, but no definite plane of division is apparent. There are now eight macromeres and eight micromeres. Each of the eight macromeres divides into two in planes at right angles to the last furrow or parallel to the second and third planes of division. This is followed later by a division in the macromere in a plane at right angles to the last or parallel to the first and fourth; but only those cells above the horizontal furrow (fourth) were seen to divide. The micromeres were not seen to keep pace with these last divisions, so that the upper (micromere) pole of the egg is covered with a mass of cells of about the same size. Sections of eggs in this stage show pyramidal figures somewhat similar to Fig. 6, but the upper pyramids are smaller, and some do not run to the centre of the egg. Each pyramid has a nucleus in its outer part, and each nucleus is accompanied by a mass of protoplasm which sends out processes into the surrounding yolk of the cell. Soon after this the formation of yolk pyramids ceases, and the nuclei (and their protoplasm) lie at the periphery of the egg. At the upper pole the nuclei are much more numerous, but smaller than at the lower, and the protoplasm forms a thick covering to the egg. Here, also, the blastoderm develops rapidly. At the lower pole there are scattered nuclei at the surface of the yolk.

The early separation of the egg into two unequal parts is apparently closely connected with the more rapid development of the embryo in the region of the smaller segment. About the time when the pyramids become lost (and perhaps at that time) each of the peripheral nuclei divides radially into an outer and an inner nucleus—each of course with its cell protoplasm. It takes place first over the upper pole, and not till very late over the lower area. This is undoubtedly the same thing as the delamination in the smaller eggs. The differences are these—that in Pallene the pyramids do not divide themselves each into two cells, but only the nuclei and protoplasm; and this takes place later at the lower than at the upper pole. The delaminated nuclei remain just under the outer cells—ectoderm—and only exceptionally do one or two wander into the yolk. These nuclei form the endoderm of the mid-gut after having devoured the yolk. The protoplasmic layer at the upper pole becomes wider and the nuclei more numerous, each nucleus being the centre of a distinct cell. At one place may be seen from surface veins an opaque area (much like the early stage of the primitive cumulus in spiders), and sections show that here an invagination of ectoderm is forming—the stomodæum. Around its periphery there is a collection of cells which are, no doubt, the beginnings of the mesoderm. The stomodæum increases in depth, and at this time the

appendages and their nerve ganglia may be seen on the surface. Above and anterior to the stomodæum are the thickenings of epiblast to form the brain. On *each side* of the invagination the first pair of appendages arises. Behind the stomodæum five pairs of large ganglia appear, and on each side of the three posterior pairs are formed the fourth, fifth and sixth pairs of appendages.

At the "lower" pole of the embryo (at this time the dorsal and posterior) the nuclei are slowly multiplying and cover the surface with thin protoplasm. Now the embryo lengthens in the antero-posterior direction, the appendages and their ganglia become more conspicuous, and there is seen a slight *invagination in the centre of each ventral ganglion.* There are five pairs of these invaginations corresponding with the same number of ganglia, and I shall call them the *ventral organs.*

Fig. 8.

Cross sections of embryos show distinctly a wide ingrowth of the surface epithelium into the centre of each ganglion. The cells of its walls are rather high, with a clear outer portion, and with large nuclei. Fig. 8 shows such a cross section. These organs close on their outer surface, and there remains in the centre of each ganglion a cavity, which is rather longer than wide from side to side, and persists till quite late in embryonic life.

I need only refer to similar (?) invaginations in Peripatus, and more especially to a section of a pair of these organs figured by Sedgwick for the ventral organs of the jaws of Peripatus (*Studies Morph. Lab.*, Cambridge, Vol. IV, Pt. I, Plate 10, Fig. 4), which easily suggests a comparison with an *early stage* in the development of the ventral organ of Pallene. Although I have looked very carefully I have not satisfied myself as yet as to whether or not there are any invaginations for the brain of the Sea Spiders. The appendages grow in length, and into each there is pushed an outgrowth from the mesenteron. These outgrowths contain yolk, and this is covered by a layer of endodermal cells. Along the ventral half of the embryo there are scattered mesoderm cells, and these extend into the appendages between the endoderm and ectoderm cells.

In Pallene the second pair of appendages, which are found in other pycnogonids, never appear, and seem to have been completely dropped from the ontogeny. The third pair of appendages (the egg carriers of the male) appear at the time when the young is about to leave the parent. Two pairs of nerve ganglia develop for these appendages, and each ganglion contains a ventral organ. Later the two pairs form a single pair with four ventral organs. The presence of these ventral organs is conclusive proof as to the erroneousness of Schimkewitsch's hypothesis, that the third pair of appendages are outgrowths of the second pair. The fourth, fifth and sixth pairs of appendages appear (as already given) simultaneously and quite early. The seventh appears a little before the embryos leave the parent. Likewise do the ganglia of the seventh appear quite late. There is in addition one pair of ganglia for the rudimentary abdomen. The yolk mass becomes smaller as it is eaten by the endoderm cells, and exceptionally a wandering endoderm cell may be found in the mass of yolk. As the yolk disappears a number of schizocoels appear in the mesoderm between the body walls and the digestive tract. Dorsally the heart appears as a simple tube. The stomodæum communicates with the mesenteron and the proctodæum forms very late—at the time when the seventh pair of appendages appear. Soon the embryo leaves the parent and no doubt crawls off among the sea weeds and hydroids to shift for itself.

*The Phylogeny of the Pycnogonids.*

It will be impossible to give here the bearing of these embryological facts upon the phylogeny of the group, and I reserve for the future a fuller discussion.

It seems to me, however, that when all the embryological phenomena are taken together they give quite strong evidence for the relationship of the Pycnogonids to the Arachnids. Dohrn and Hoek have each recently reached independently the belief that the group must be considered an isolated one, with a more or less independent origin from the Annelids. I hesitate before offering an opinion against those who are so well qualified to speak authoritatively on the subject. On the other hand their opinions are based largely on the adult anatomy of the group, as little or nothing has been known concerning the germ layers, &c., of these animals; and it is chiefly on embryological grounds that I believe a comparison with the other groups of Anthropods must be based.

It is generally believed that the adults are in many respects degenerate and adapted to a very special habitat—the abdomen has become lost, or almost so, and all traces of respiratory organs are gone, the general surface of the body functioning as such: also that the group is an old one, and not derivable from any existing groups of Arthropods. So far we are together. Without going into details, it does not seem probable that the group is closely related to the Crustacea, nor very closely to the Insects. Here I can only use the *tout ensemble* of the above facts as evidence for this statement. We are then left to decide between an independent origin for the group and an alliance with the Arachnids. If there are any special reasons for an alliance with the Arachnids, I believe such facts must turn the greater weight of evidence towards such a relationship. Briefly then in this connection these considerations must be given:

1. The process of *multipolar delamination to form the endoderm* is, I believe, common to the two groups. We have it represented in its greatest simplicity in the majority of the Pycnogonids, while Pallene furnishes an analogy to the changes which an accumulation of food yolk will cause in this process, and renders a comparison with the Arachnids quite possible. I will refer to Metchnikoff's figures for Chelifer, and to Balfour's embryology for the Spiders (Vol. I, page 119, Sec. Ed.). Here we read: "It appears to me probable that at the time when the superficial layer of protoplasm is segmented off from the yolk below, the nuclei undergo division, and that a nucleus with surrounding protoplasm is left with each yolk column." Compare Fig. 6 and 7, and see account of Pallene.

2. The formation of an opaque area (Pallene) at the place where the stomodæal invagination appears.

3. The early formation of *mesoderm at this place*—the primitive cumulus of Spiders. (?)

4. The general mode of appearing of ganglia and appendages.

5. The body cavity of the appendages and the early presence of mesoderm.

6. The formation of *endodermal pouches* from the mid-gut into the appendages, these pouches *containing yolk in the embryo.* Compare Chelifer and Spiders.

7. The large "upper lip" of Chelifer suggests an homology with the proboscis of pycnogonids.

8. The first (Chelate) appendages appear at the sides of the stomodæum and subsequently move forward, and are innervated from part of the supra-oesophageal ganglia (brain). They will in this bear out a close comparison with Chelifer (or with Arachnids.)

9. The lumen of the invagination of the stomodæum is triangular in

outline and remains so in the adult. Schimkewitsch describes a similar triangular invagination in the Spiders, and compares it directly to that of the Pycnogonids.

The full meaning of the ventral organs I cannot discuss now. I have compared them to similar organs of Peripatus. It may be that in this respect the Pycnogonids show a very primitive structure, common to them and to Peripatus, and if so, traces ought to occur most probably in other Arachnids.

The absence of brain invaginations would be a more weighty objection against the relationship of the two groups, and really the only good objection I know from the embryology.

The openings of the reproductive organs of the adult on the legs cannot be fairly urged against my comparison, for we have so far no explanation of the meaning; and on the other hand this gives little better foundation for a relationship with the Annelids.

All the above comparisons are not of equal weight, and some may be wrong; but taken all in all, I must appeal to them to bear out the hypothesis of the relationship of the Pycnogonids to the Arachnids.

Baltimore, March 15, 1890.

A Contribution to the Embryology and Phylogeny of the Pycnogonids.

In the year 1767 Karl Linné in the twelfth edition of his Systema Naturae described under the name of Phalangium, a Pycnogonid & here for the first time is the question raised whether the group is to range under the Arachnids or the Crustacea.

A hundred years elapsed and the problem remained unsolved; the group was placed now here, now there, now amongst the Crustacea & next amongst the Arachnids.

Then Prof Dohrn attempted the solution from the standpoint of Embryology, instituting a comparison or even identity between the Pycnogonid-larva & the Nauplius, believing the Pycnogonids to have diverged from the Crustacea at this point.

During the following twenty-five years opinions once more vacillated between Arachnidan & Crustacean affinities. Recently Prof Dohrn & Dr Hoek have each independently monographed the group, placing the morphology of the order on a very firm basis.
Independently likewise they each reached the conclusion that the group is to be placed neither with the Arachnids nor with the Crustacea, & the ~~two~~ groups have come down in parallel lines
The early stages of the embryology of the Sea-spiders have been practically untouched, & before any final descision, as to the affinities of the group is to be made, these stages in the developement should be known & take equal rank with Comparative Anatomy in disentangling the affinities of the group.

For many reasons the present paper attempts in no way to give a complete answer from the embryological side. The very great difficulties of technique had slowly to be overcome, the time at command prevented a detailed description of the different organs arising from the germ layers, so that much remains that might be done.

In the Summer of '89 material for work was collected at Woods Holl, Mass. Through the courtesy of Prof Mac Donald I was enabled to collect & study at the station of the U.S. Fish Commission at the this place. To Prof Mac Donald I am also indebted for many other kindnesses extended during my stay at Woods Holl. Three genera of Pycnogonids — each with a single species — are to be found at this place, viz. Pallene empusa, Phoxichilidium

maxillare Smith (Ammplodactylus dentus. Wilson) & Tanystylum orbiculare. During July, August, & September these are found with eggs. Pallene inhabits the hydroids (Tubularia, Pennaria) on the piles of the wharves & is common on the red-sea-weeds below low-tide mark. The hydroids or sea-weeds as soon as collected were brought into the laboratory & worked over piece by piece. Each bunch was in turned swished rapidly backward & forwards in a dish containing a small amount of water so that the Pycnogonids were shaken loose & could be easily picked out. The other genera were more easily found & on separating the masses of hydroids it could be easily seen clinging to the stems. The males of Pallene carry on each pair of ovigerous legs a small

bunch of eggs. Each bunch contains from one or two to fifteen or twenty eggs. The eggs of Phoxichilidium & Tanystylum are individually much smaller than the last, but are very numerous so that the bunches are much larger especially so in the former. Phoxichilidium carries several bunches strung along on each ovigerous leg of the male, the bunches are white and very conspicuous against the purple color of the adult. Tanystylum has smaller bunches of eggs with the individual eggs large, & the masses are carried so that they form a circle of clusters held against the ventral side of the male.

The adults with eggs were put into alcoholic picro-sulphuric acid for several hours & then gradually carried through different grades of alcohol of increasing strength.

Other methods of hardening gave far less satisfactory results i.e. boiling water or Flemming's solution

To prepare the eggs & embryos for study they were passed through absolute alcohol (1. hr). turpentine (2.-4. hrs), soft paraffine (1. hr), hard paraffine (1.-2. hrs.) They were cut in paraffine & fixed to the slide with albumen fixative Then back again through turpentine, absolute alcohol, 95%, 80% 70% alcohols to Kleinenberg's Hæmatoxylin where they remain for a very long time (12-48 hrs). Then washed fifteen minutes in acid alcohol & up again through the alcohols to turpentine & into balsam. In Pallene each eggs was, in many cases, pricked with a very sharp needle before going into absolute alcohol, It is necessary to do this under a dissecting microscope.

By these methods very excellent results were often obtained & after many failures of other methods was found to be the only satisfactory one
In Pallene the larger size of the egg makes a study of the earlier stages much easier but the other genera have a much simpler developement & it seems better to give first an account of these.
To Prof W. K. Brooks I am greatly indebted for help & suggestions during the work.

Tanystylum & Phoxichilidium
The eggs of Tanystylum measure .08 mm in diameter (in preserved specimens) & those of Phoxichilidium .05 mm.
In both animals there is a regular segmentation. In Plate III. figure a is

a surface view of an egg of Phoxichilidium, divided into two equal parts; in figure b an egg into four cut with the segments shifted around, & figure c an egg into eight equal parts. Similarly figures d & e for the two & four cell stages of Tanystylum. The eight celled stage I did not obtain for this species.

Figure f is a surface view of an egg of Tanystylum at about the twenty-four celled stage & an optical section of an egg at this stage shows each cell to run from the periphery to the center of the egg where they all come together at a point. Each cell is thus pyramidal in shape & contains a single nucleus. In Plate 1 figure 8 there is a section of an egg at a later stage than the last. This and the following sections

are from eggs which were cut in paraffine. The section is a later stage than the preceding surface view so that the pyramids are narrower than before.

Figure 11 shows a somewhat older stage for Proxenilidium. Very soon after this — perhaps after the next cleavage — a most important change takes place in the egg. I have not seen the actual change in the living egg but serial sections leave not the slightest doubt as to the process. Each nucleus divides radially into two & this is followed by division of each pyramid into two parts in a plane at right angles to the radius, of the circle, lying in that pyramid. This is shown by Plate I figure 9 for Tamystylum.

Here it is seen that by a process of

multipolar delamination the egg divides into two germ-layers — an outer peripheral circle of cells & an inner mass of cells; these latter soon round off & leave no trace of the former pyramidal arrangement. In figure 9 one cell is still seen running from the periphery to the center. This section does not show a nucleus in the inner part. The inner cell I shall speak of as the entoblast & the outer circle as the ectoblast. This figure -9- is somewhat diagrammatic in as much as only part of the inner cells is shown for usually they are more closely packed together than here shown; & in this case it is due to a part of the section having broken away (redrawn in figure) & set some of the inner cells

In figure 11 is a more accurate drawing of an egg of Tamystylum immediately after delamination has taken place. Exactly similar changes were seen in the eggs of Phoxichilidium, but the figures first given serve in every respect for both species. The central as well as the peripheral cells continue to divide but soon the entoblast cells loose their well defined boundaries & the nuclei seem in part to disappear. The result is that we have in the center of each egg a granular yolk with scattered nuclei in it. Here & there is an indication of a cell boundary. During this time the ectoblast cells have divided tangentially & have become much smaller yet at all times a distinct boundary remains between ectoblast &

ectoblast. Figure 12 for Phoxichilidium & was an embryo at this stage.
It is here seen that the ectoblast cells over one hemisphere are somewhat higher than at the opposite & I find this very constant in sections of both species at this stage of developement
After this it becomes difficult to follow out the fate of the germ-layers. The outer cells become smaller & flatter to form the ectoblast & the inner cells arranged into organs the most conspicuous of which is the digestive tract.
There is a triangular invagination to form the stomodaeum & the proboscis appears between the first pair of appendages which have now begun to form.

These appendages are very conspicuous in surface view where they project beyond the surface of the body. Between them appears the slightly projecting proboscis & about the middle of the embryo are seen the second & third pairs of appendages which are small and inconspicuous. Dohrn has given excellent figures of embryos at this stage both in his earlier paper & in his later monograph. Soon after this the egg coverings swell up somewhat & the embryos finally break out of the egg, so that the appendages now can straighten out. In Plate IV. figure IX is a surface view of a larva of Nymphon as seen from the ventral surface. Dohrn speaks of this as the Pantopod-larva & Hoek calls it a Protonymphon

Its general characters are shown in the figure. There are three pairs of appendages the first pair chelate with the movable claw working outwards & downwards, the second and third pairs have, distally a sharp spine, in the middle of the limb a large segment & proximally a prolongation of the body which may be regarded as the basal segment of the appendage. Between the first pair of appendages the proboscis projects forwards, with the mouth opening at its distal end. Behind the base of the proboscis is seen the pair of ventral ganglia From there the circumoesophageal commissure ascends upwards around the oesophagus & laterally are given off on each side a pair of nerves to

the second and third pairs of appendages. Dorsal to these ganglia — four in all, the two pairs being fused, is seen the outline of the mesenteron which ends blindly behind.
About the middle of the embryo, just back of the pair of ganglia is seen a pair of oblong masses which are the beginnings of another pair of ventral ganglia.
In the basal joint of the first pair of appendages is an opaque mass composed of large cells, from which runs out a duct towards the base of the spine and Dohrn has traced it out to the very tip of the spine, where it opens to the exterior. This organ is a gland and its duct is the long tube in the spine

A dorsal view of the embryo shows the brain, just above & a little in front of the ventral ganglia. On its upper surface are a pair of small pigmented eyes. A transverse section through the body of this Pantopod-larva is shown in Plate 1. 13. It passes through the center of the body & cuts below the the large ventral ganglionic mass, & passes through the base the the third pair of appendages. Above it cuts the posterior part of the brain. In the center of the section is the digestive tract. This is cut at a point where it is about to give off diverticula to the first & third pairs of appendages.
The first of these is marked D' & the second D".
Below the digestive tract

pair of ganglia which sends out nerves to the corresponding appendages. Above the digestive tract the section at B cuts the posterior part of the brain. The cavity of the body has a few scattered mesoblast cells in it & a few bits of broken muscle fibres. These fibres in the living embryo seemed to connect the the mid-gut to the body-walls.

In the base of the legs are seen several cells which at M are arranged, in part, around a central cavity. This cavity does not seem to connect with the mid-gut & it seems very probable that it represents the body cavity in the legs, that the surrounding cells are of mesoblastic origin. In Pallene as we shall see later there are

similar cavities which are undoubtedly mesoblastic in origin.
The mid-gut ends blindly behind as is seen in other sections.
In figure 14 is shown part of a section through a more anterior part of the body. The section passes through the brain above & the first pair of ganglia below. These two are connected by the circum-oesophageal ring. This commissure is composed of both cells and fibres.
In the next section to the one figured a broad band of nerve fibres passes on each side from the brain to the ventral ganglia & in figure 14 a few of these fibres may also be seen.
In the middle of the commissure lies the cross section of the oesophagus. Its lumen is triangular and its wall

composed of a layer of cells which are clear around the periphery of the triangle. Around the oesophagus are a few scattered mesoblast cells. From the brain B there is part of its substance which projects ventrally towards the oesophagus o is quite conspicuous in sections of the Pantopod-larva in this region.
On each side of the brain are seen a pair of diverticulae of the mid-gut. These go to the first pair of appendages o are traceable to D' of figure 13.
The first pair of appendages are as Dohrn has shown innervated from the brain.

The section of the embryo following figure 13 give a cross section of the pair of simple eyes. A part of

this section is shown by figure 15
In the middle line of this section above the posterior part of the brain B the ectoblast is thickened beneath the cuticle & immediately on each side of the middle line appear the sacs of eyes. Each is seen in section to be composed of three cells – two clear outer ones with large nuclei & an inner much pigmented cell. Around the eyes the ectoblast is quite thick & on each side it sinks down slightly from the surface, suggesting that the eye may be here increased in size.
In figure 16 is a section through the third pair of ventral ganglia, which are say on the ventral side of the embryo posterior to the fused pairs of first & second

ganglia. The section shows that at this place the epiblast is greatly thickened & the cells columnar with clear outer portions. In the ganglion on the left of the section the cuticle suddenly dips down into the center of the ganglion where it becomes extremely thin. This was not so clearly seen in the right hand ganglion but traces of it were seen here also. These structures I shall speak of as the Ventral Organs & we shall come across them again in Pallene where they are worked out in greater detail.

Pallene empusa.

There is great variability in the size of the eggs in the ovigerous legs of the males. The average size

of these which seem to be normal eggs is .25 mm; but often bunches contain one or more much smaller eggs, some of which seem to begin to develope. These very small eggs are most probably immature & accidental. Although the eggs of Patella are much larger than in the preceding animals — having 125 times the volume — yet the yolk is almost transparent so that nuclear divisions of the segmenting egg are easily seen from the surface.
The adult is remarkably transparent & consequently most difficult to see as it rests quietly amongst the hydroids or sea-weeds. It seems that the eggs have adapted themselves for purposes of protection by thus becoming

transparent. Some or less time necessarily elapses after the animals are collected before they can be examined so that I have been unable to see the extrusion of the polar bodies. The nucleus of the egg & its accompanying protoplasm is extremely large & situated near the center of the egg.
Each division of the nucleus is accompanied by a division of its surrounding protoplasm so that in surface views it is impossible to separate the one from the other. In the figures of Plate III the darker masses in each cell indicate the position of the nucleus & protoplasm but for the sake of brevity I shall speak of this simply as the nucleus

In the unsegmented egg the nucleus is seen to elongate & to divide into two halves & this is immediately followed by division of the egg itself into two parts. The first furrow divides the egg into two unequal segments. Figure A Plate III shows an egg after the first division. Each segment contains a single nucleus (Hoek has made a different observation from this, see infra). After this first segmentation the segments flatten somewhat & remain so during the resting period. The second division came on about three quarters of an hour (to an hour) after the first. The nucleus of the smaller segment — the micromere — divided first & then the segment itself into equal parts

This was followed five minutes later by the division of the nuclei of the large segment — the macromere — & then the macromere itself.
In figure B an egg is shown as seen from above after this second division which is indicated by 2 – 2.
The plane of segmentation of the micromere & macromere are drawn in this figure as though they coincided. but this is not the rule. The plane of segmentation of the micromere may be turned at as much as 30° (& exceptionally about 45°) to that of the macromeres. I think it should be considered as one & the same plane & one & the same division, it spite of individual variations.
The segments again flatten together

& after an interval of about an hour the third division commences. The plane of division is at right angles to the last & is shown by figure C in which the egg is seen from above. Again the plane of micromere & macromere do not quite coincide; the number 2-2 indicate the second division & 3-3 give the plane of the present (third) division. This plane is a zigzag line lying between 3-3. If we examine the opposite pole – the lower – of an egg at this stage we find the large macromeres come together as shown in D although there are many differences in this respect. So far the planes of division of micromere & macromere have been supposed to coincide or to be referred to the same

division plane but after this stage is reached (8 segments) the planes cannot be considered identical. About an hour after division division the fourth rythm comes on. This division plane is shown for the macromeres in side view in figure in E, by the line 4-4 and is seen to be parallel to the first plane of segmentation 1—1 The four macromeres become eight. About the same time — may be five minutes before or after — the micromeres divide. In figure E they are drawn after division has taken place and figure F shows how these cell are divided — the curved lines indicating twin-cells As we see from the very nature of the division of the macromeres

it is impossible to have their plane of division to correspond with that of the micromere and the division lines of the latter lie in a plane at right angles to the plane of division of the micromeres We have now eight macromeres & eight micromeres after a resting period of about an hour the fifth rythm begins.
The nuclei of the macromeres of figure E show by their elongation how they are to divide & the plane of division lies between them or at right angles to the last division plane.
Fig C shows the egg after division into eight micromeres but the micromeres had not as yet divided & remain eight in number. Soon however they do divide but no definite

plane of division of all of the segments was discovered. There are now 16 macromeres & 16 micromeres.
The next plane of segmentation of the macromeres — at the eighth rythm comes on after another resting period of an hour. This is shown by figure H at 6-6.—6-6. The two planes are at right angles to the last two (5-5) and are parallel to the first & fourth (1-1. 4-4)
I did not see the sixteen micromeres divide into thirty-two nor could I trace them further — there are 32 macromeres & 16 micromeres, or in all 48 cells.
After an hour's interval the macromeres lying between the planes 1-1 & 4-4 in figure H were each seen to have two nuclei but this

did not seem to be the case with the macromeres of the lower pole. The egg had been under observation for many hours & did not develope farther so that this last attempt at division in the upper macromeres may have no special significance. Besides the general facts of segmentation as just given, several interesting variations in the method of segmentation of the egg were clearly made out. In the example given above the micromeres divided first (at the second segmentation) giving two micromeres & one macromere. In two other observations this was also true but in three other cases the macromere divided five minutes before the micromere. And again in the last case

the two macromeres divided into four before the two micromeres divided into four. so that the greater amount of yolk of the macromere did not seem in itself to retard segmentation. In several later stages (32, micromeres & 16 micromeres) the rythm of macromeres & macromeres given above did not so closely correspond but the micromeres seemed to drop behind.

If the accumulation of yolk has been a very recent event in the egg of Pallene & the variations in size may bear this interpretation — these differences in the method of segmentation may be due in part to the segments of the egg struggling to give synchronous beats at each rythm but being hampered by the presence of the yolk

If the first plane of segmentation of Pallene correspond with the first plane of division of Phoxichilidium or Tanystylum — and a priori this seems most probable — is it not conceivable that the acquisition of yolk to one half of the egg might cause great changes in the synchronism of segmentation of the two parts; & if so it is easy to imagine we have here an egg in a period of variation — that one or another of the above changes may become fixed for the species?
Later stages of segmentation than those described are difficult to follow or to distinguish between macromere & micromere of the upper pole but in general the cells around the upper pole

smaller & more numerous than at the lower. Figure H Plate III shows the ventral (or macromere) hemisphere of an egg at a later stage than any of the preceding. The outer ends of the cells, those seen in the figures are polygonal & the nuclei lie very near to the surface. The whole cell is pyramidal in shape with its apex at the center of the egg & its polygonal base at the periphery of the egg, with the nuclei in the base of the pyramids. Each nucleus is still accompanied by a surrounding mass of protoplasm & it is without doubt this protoplasm which is seen from surface views. At this time the cells of the lower pole rarely divide & remain

for a long time almost constant in size & number, but the cells at the upper pole undergo rapid changes & our attention must now be turned almost entirely to that region.
The next change which we can see in surface views is at the upper pole where a whitish opaque area is forming, & which may be profitably compared to the similar formation in Spiders eggs & called there the Primitive Cumulus. This is due to an accumulation of cells at this point where an invagination is about to take place to form the stomodaeum. Soon there are other opaque areas formed at the surface, which are seen to occupy definite positions and are the thickenings

for the brain, ventral ganglia & appendages. These are shown in figures I & II Plate IV. In figure I we have a surface view of the head region of a young embryo. In the upper part of the figure are first the two oval thickenings to form the brain or supra oesophageal ganglion. At this stage they just touch in the middle line. Below this and in the middle line is the thickening of the stomodaeal invagination. In the center is a triangular shaped cavity — the cavity of the invagination. The base of the triangle is towards the brain. On each side are the thickenings of the first pair of appendages. In the lower part of there is a slight depression which indicates the line between the claw

& the next segment of the limb against which it works. Posterior to these various thickenings appear two rows of opaque areas, the nerve ganglia
Three pairs of these are seen in this figure, the first two being somewhat smaller than the third.
On each side of the last pair appear part of the thickenings of the first pair of ambulatory legs (the fourth pair of appendages.
Figure II is a continuation of the last figure & shows the ventral & posterior part of the same embryo.
The upper pair of ganglia are the second pair, & were seen in figure I & the second pair of this is the third of the last figure. On each side of this third pair of ganglia are again the first pair of walking legs

Two more pairs of ganglia follow this third. On each side of the fourth or fifth pairs of ganglia appear the second or third pairs of walking legs in embryo at a stage later than the last is shown by figure III.
Here the embryo has elongated in an antero-posterior direction so that the figure shows only the ventral side of the animal. Figure IV is a dorsal view of an embryo at the same stage These figures show that the region about the stomodaeum has grown forward with the opening of the stomodaeum at its distal end This outgrowth is seen in the figures as a forward prolongation of the embryo in the middle line. On each side of it are seen the first pair of appendages which have

grown forward.
On the ventral side of the embryo appear on each side of the middle line five pairs of large ganglia. See figure III. On each side of the last pairs pairs appear the three pairs of walking legs, which are longer than in the last figure, are bent & stand out from the surface of the embryo. Posterior to the last pair of ganglia the embryo has a thickened mass of undifferentiated substance.
In a dorsal view — figure IV — we see the brain & behind it the large yolk mass of the embryo.
The two halves of the brain have come together & each half is slightly lobed. Around the periphery of the yolk appear the six pairs of [illegible]

o behind the thickened posterior mass of the embryo.

Returning to the ventral view of the embryo — figure III there is seen a most interesting structure in the center of each ganglion. Each is an invagination of the surface into a ganglion o these invaginations are elliptical in outline with the long axis corresponding to that of the embryo. These structures I shall call the Ventral Organs o by means of serial sections we shall later study them in more detail

In the next stage, shown by figure V the embryo is more oval in outline. The appendages have also elongated & become more bent. The posterior pair have begun to grow forward between the more anterior pairs. The

important change is in the fusion of the first two pairs of ganglia which now appear as one pair of rather large ganglia. This pair of ganglia still shows its double structure by the presence of two pairs of ventral organs. The third pair of ganglia also shows a pair of ventral organs but the more posterior ganglia are covered by the posterior appendages so that these ganglia cannot be seen from the surface.

After this stage is passed the appendages grow enormously in length & the embryo becomes flattened from side to side.

A figure of an embryo at this stage is shown, in side view in figure VI. The first appendage is chelate & has a

joint near its base & one also sees it has moved more dorsally to the proboscis.

Beyond & beneath this appendage appears the proboscis which has much elongated. Near the base of the appendage is seen part of the brain this figure also shows that the yolk mass is seen to continue into the center of each ambulatory limb

The three pair of legs are much bent & each ends in a spinose tube process. The body is seen to end behind in a knot like projection. The neural ganglia are shown between the bases of the legs & the height of each at this stage is about equal to its length.

In older embryos the yolk begins to

disappear & the sides of the embryo to become thicker. After this the embryo lengthens a great deal the appendages grow much longer & become segmented. Another pair of appendages appears behind the last pair of walking legs & the knob-like projection at the end of the embryo is pushed more dorsally to form the rudimentary abdomen. Four pairs of eye spots appear over the posterior end of the brain. After these changes have taken place we reach a stage shown by figures VII & VIII

The first figure is a ventral view of the embryo at a time when it is ready to leave the parent. The three pairs of segmented walking legs

become straightened out at the sides of the body. In the figures only the proximal ends are shown

The fourth pair of walking legs appears at the posterior end of the body

The first pair of appendages — the chelicerae are now attached quite dorsally to the proboscis which appears between & below them. Each has three segments including the terminal one which acts together with the second to form the pincers.

On the sides of the body just in front of the first pair of ambulatory legs are a pair of projections, one on each side These are the beginnings of the third pair of limbs — the ovigerous legs.

I have seen no traces of the second pair of appendages in the ontogeny of Pallene.

Five pair of large ganglia lie along the body & in addition a small seventh pair.

The first pair as we have seen is double & composed of the first & second pairs. The next pair - the third - is between the first pair of ambulatory legs, the the fourth pair of ganglia lies between between the second pair of legs; the fifth near the base of the third pair of legs & the sixth, each of whose ganglia is smaller than those in front, at the base of the fourth pair of legs

The small seventh pair of ganglia belongs to the rudimentary abdomen & does not lie in a plane with the more anterior ones but lies the sixth is dorsal to the one in front of it as partially shown in the figures.

The oesophagus is seen to start at the distal end of the proboscis & to disappear in the body where it is not easily followed on account of its transparency.
The prolongations of the mid-gut into the legs is not shown in the figures except for the last pair of immature legs
In figure VIII is a dorsal view of the same embryo. Four pairs of large ventral ganglia, and in addition the small rudimentary ganglia of the abdomen. The fourth first & second pairs are hidden by the brain.
On the surface of the brain are seen four small pigmented eyes.
The oesophagus is triangular in shape in cross section with the broad base turned upwards & this base is seen pro[illegible]

surface. At the posterior end of the animal the rudimentary abdomen is seen & at its end is the opening of the anus.

Internal Changes.

Sections of the early stages of segmentation give little information in addition to what we see from surface views. They show that each nucleus is contained in a separate segment & that many of these segments turn to the center of the egg. Thus cells derived from the first micromere cannot reach to the center of the sphere.

Figure 1. Plate 1. is a section of an egg at this stage when there are thirty-two micromeres. The upper part of the figure is probably in the region of the micromeres. In the center of this

appears a clear cavity either in yolk but this is not constant for all eggs. In some it is certainly absent but I am unable to say whether or not it is caused by hardening reagents.
What seems to be a similar cavity is found in the eggs of some spiders. The whole egg is divided up into the segments in the form of pyramids. In some of them in this figure can be traced to the center but other sections show each pyramid of the macromeres to have its apex at or near the center of the egg.
The nuclei are situated around the periphery of the section o the protoplasm which invariably accompanies each nucleus sends out fine pseudopial filaments into the surrounding yolk

Figure 2 is in the same stage as the last & undoubtedly passes through the micromeres at the upper pole. These micromeres & their nuclei are seen to be smaller than the cells elsewhere & the pyramids are seen to fall short of the center of the egg. There is no central cavity present in this egg.

Sections of eggs somewhat older than the last show that the nuclei of the upper pole have rapidly increased, & that they have migrated to the surface of the yolk which loses its pyramidal structure over the upper surface.

The protoplasm surrounding each nucleus fuses with that of surrounding nuclei, though how close such fusion is formed I cannot say

Such a condition is shown in figure 3 where the protoplasm form a cap over the upper surface of the yolk. The nuclei in this section are abnormally large which is probable, due to the hardening reagents, but the section seems normal in other respects. The lower area of the same egg shows three or four scattered nuclei near the surface of the yolk. At this stage of development there is a single layer of cells at the surface of the yolk. Between this stage & the next which I have figured there is a gap. In this next section, figure 4 we see the number of nuclei at the upper pole to be more numerous than before & much smaller. The protoplasmic cap has become larger

& its protoplasm is for the most part without the amoeboid processes of the last figure.

A very important change has taken place between these two stages, viz the formation of an inner layer of cells. Within the area of the cap appear a few somewhat flattened cells in figure 4, & these send out processes into the underlying yolk. Two of these cells are shown in this figure. I have not made out any definite arrangement for these cells but they seem to lie only under the upper surface of the embryo. Where these cells come from & at what time they appear must in part be a matter of conjecture but much light is thrown on their possible origin by a

study of somewhat older stages.
In figure 5 is a section of such a stage. The number of nuclei in the outer germ layer has nearly doubled and the area itself covers a much greater surface of the egg than in the last stage.
Under the blastoderm are seen five inner cells, with their pseudo-podia extension. The larger number of these cells here than in the last figure is due in part to the greater thickness of the sections. At the lower pole are the [illegible]. There below is the outer germ layer, although they show (as did all the outer at an earlier stage) the protoplasmic extensions into the yolk. This section itself throws little light on the cells of the

inner layer but in other sections at a similar stage I have found what seems to furnish the solution of the problem. From such sections I have drawn figures 6 & 7.
These are taken from the periphery of the cap of cells at some such point as P in figure 5. Figure 6 shows two cells which have just separated from the outer layer of cells & we also see beyond them a single mass of protoplasm with two nuclei which presumably have just divided.
I have not seen any karyokinetic figures in nuclei dividing in this direction & it is possible we have here a direct division as Heider has recently shown in Hydrophilus at a similar stage of development.

although it is equally as possible it is due to poor preserving-agents
Again in figure 7 we see a single mass of protoplasm with two nuclei which have just divided. These I believe to give a clue to the origin of the inner cells of the preceeding figures & to point out that they too have had a similar origin from the outer layer
Keeping before us this process of delamination in Phoxichilidium &c I think we may regard these inner nuclei of Pallene to have come from the outer cells by delamination & even that we may push the comparison a step farther & consider that each cell of the outer layer to have given rise at one time in its history to an inner cell

o then that the outer cells continue to divide tangentially to form the blastoderm. The reasons for such a belief are there. In cross section the number of inner nuclei are slightly in excess of the peripheral nuclei of the lower pole. See figures 4. & 5. As the outer cells of the upper pole were at the beginning more numerous than the peripheral cells of the lower pole we ought to get, if the hypothesis be true, exactly what we do find.
Further, at the periphery of the blastoderm where the inner cells of the lower pole are added on we can always see such a method of multiplication taking place.
The differences between the

that in Phoxichilidium are there;
that multipolar determination does
not take place simultaneously in all
the cells at once but in Pallene
slowly progresses as the cap of cells
makes its way to the lower pole
of the egg, incorporating into itself
as it goes the outer cells which are
cells as they are added on first pair
off an inner cell
After this stage we pass to older
embryos where there two layers
- ectoblast & entoblast - begin to
differentiate into organs.
The first to appear is the stomodaeum
which results from an invagination
of ectoblast. This is shown by figure
17 Plate II Here it is seen the ectoblast
at one point has pushed inwards a crowd

the periphery of the invagination appear several cells with branching & anastomosing pseudopodia. These I believe to be the first appearance of the mesoblast.
A few of the cells drawn in the figure belong without doubt to the entoblast & at this stage it is difficult to separate the two.
The section passes longitudinally through the embryo; & just ventral to the stomodaeum there is a thickening of the ectoblast to form the first ventral ganglion. Under the ectoblast are found much branched entoblast cells which are still comparatively few in number. Whether the circum-stomodaeal mesoblast comes from ectoblast or entoblast I am unable

to say. Dorsally to the epiblast the epidermis continues for a short distance & then becomes exceeding thin. From this stage we pass to embryos of the age represented by figures 1 & 11. Plate IV. The first figure, 18, is a cross section through the stomodaeum of 1 (see line 18 of the figure) The invagination is deeper than in the last section & its lumen is closed The ectoblast cells of its walls are two layer thick. On each side of this central invagination are what appears to be a lateral invagination. These supposed invaginations have given me endless trouble & even now I feel some uncertainty as to my interpretation of them. On each

side of these is seen the thickened ectoblast of the first pair of appendages. The lateral ingrowths are I believe caused by the growth of these appendages which tend to grow outwards as they increase in size but are prevented from doing so by the the egg coverings & the result is that the ectoblast becomes folded on itself to make room for the growing appendages. This view is strengthened by the presence of somewhat similar imaginations at the side of the other appendages.

This part which is pushed in would correspond to the dark furrow between each appendage of figure I & the cells forming the stomodaeum. The mesoblast around the stomodaeum

& under the appendages has increased & is now clearly distinguishable from the inner covering of the endo-blast, which lies only at the periphery of the yolk & between it & the mesoblast. In figure 19 we have a section from the same series as the last, but more anterior & through the region of the brain corresponding to line 19 of figure I. The section is entirely in front of the stomodaeum & cuts the two brain-thickenings of the surface view. Here again the ectoblast is seen to be distinctly folded & this folding (invagination!) is directly continuous with the last. At first sight this seems nothing more than a forward continuation of the last groove but it is not because the folding of the appendage should exist

my influence over that part of the brain. Again it might be interpreted as folding due to the brain but I can see no good reason why such thickenings — not outgrowths — should produce the groove. There is one other possibility viz that these may represent invaginations into the brain itself. Against such a view is the absence on surface views of any such invaginations & also that the folds are directly continuous with, & quite similar to, the groove between the stomodaeum & the appendages; so that I can not hold this either as a true solution.

Beneath these ingrowths appears the pair of thickenings for the brain which are seen to be continuous across the middle line. On the inner surface of these lobes are seen a few ento-blast cells as shown.

The next figure, 20, passes through the middle of the brain, but is farther forward than the last. See line 20 Fig I Plate III which indicates the place of the section. The cells of the ectoblast seem to pass into those of the brain. Sections still farther forward, where the two lobes are still cut show the brain thickenings on each side & seperated from each other.
We see in surface views of embryos at this stage that the ventral ganglia have appeared & figure 21 is a section through two of them, the first pair. But only do we see that the ectoblast has greatly thickened in two places on each side the middle line but the outermost cells of each mass show certain peculiarities. They are much elongated at right angles to the surface & their outer points come together at the middle point of the surface of the

ganglion. The left hand ganglion in the figure is cut through this central point & the ganglion on the right a little to one side. The nuclei lie in the inner parts of the cells & the outer parts of the cells are clear & transparent while their inner ends are more granular. This difference in the parts of the cells is very constant through the later stages. The cells form a structure which I have called the Ventral Organs.

In figure 22 is a section of a pair of ventral ganglia from an embryo at stage III. Here there is in the middle of each ventral ganglion a wide invagination lined by columnar cells with their clear outer portions turned towards the cavity of the invagination. The nuclei in these cells are larger than those in other parts of the ganglia & are seen quite often in process

of karyokinetic division. The spindles of the dividing nuclei are in some at right angles to the long axis of the cells or in other parallel to this axis.
A narrow connection of small cells runs across the middle line from ganglion to ganglion. The next figure, 23, is from an embryo at about stage V. The outer edges of the invagination have turned in until they have nearly met above the cavity of the invagination.
In other respects the section is similar to the last. At the next stage, shown by figure 24, the arching over is completed & fusion has taken place so that there is a cavity in each ganglion. Each cavity does not run through the whole length of each ganglion but lies only in its middle portion. There is no communication between the cavities

of different ganglia. In this figure each ganglion has increased in size & the cells have become more numerous & further the neighboring ganglia are connected by a cross commissure of fibres. Further the nuclei of the outer cells (those lining the cavity) are now more like the nuclei of the ganglion cells later stages show that the central cavity of each ganglion disappears although they seem to persist for quite a long after they have been enclosed by the ganglia. That this structure may have functioned as an organ in some ancestral form, I believe possible first because they are distinctly marked differentiated before any invagination takes place, secondly because their cells are histologically distinct from the surrounding ectoblast & from the cells of the ganglion beneath & lastly from

the arrangement of the cells which suggests a sense organ comparable to the simple ectodermal organs of many animals. It also seems probable that we have exactly similar structures in the Pantopod-larva of the other Pycnogonids. Returning to stage III we have a cross section of the body drawn in figure 25. The section passes through the middle of the body in the plane of a pair of walking legs. The large mass of yolk is still seen filling the upper part of the embryo. Over the ventral surface of the yolk, the entoblast cells form a continuous covering and are indicated by N in the figure. At the base of the appendage the entoblast sends out a prolongation which is filled with yolk while the entoblast cells are here higher

& more closely packed than elsewhere.
Into each of the six walking legs is a similar prolongation of entoblast from the mid-gut. Beyond these diverticula there is in each leg a definitely marked cavity in the mesoblast. In figure 25 the surround mesoblast is shown by M.
As the prolongations of the mid-gut push into the legs, these cavities cannot be made out & have either become lost or are to complicated to follow out.
Besides these cavities which would seem to be body-cavities we shall come to others later in development which seem to be schizocoels. The surrounding mesoderm of these is irregular & quite different from that around the body-cavity proper.
The ectoderm over the appendages is thicker than elsewhere. The ventral ganglia at

this stage have in most cases the ventral organs
although in this figure none are shown
& they have crossed to the back.
The ectoblast of the dorsal surface is quite
thin & the mesoblast has not appeared
in that part of the animal
In figure 26 is a drawing of a cross
section through the head of an embryo
at a stage a little later than III but
not so late as IV The section
passes through the brain above & the
second pair of ganglia below. Between
the brain & the ventral ganglia the
stomodaeum is seen. Its lumen
is seen to be triangular in outline
with its base turned upwards.
On each side of the stomodaeum appear
cross sections of the first pair of gut-
diverticula. The single row of endoblast

cells surrounds the central mass of yolk. Scattered mesoblast cells are found around & between these different structures leaving here & there openings between the cells. Such schizocoels are shown by SS in the figure.

Going on to stage V we find that sections give little more than was seen in the preceding figures. The prolongations of the mid-gut into the legs have grown longer & as seen from surface views the first & second pairs of ganglia have fused.

In stage VI the yolk-mass continues to fill the central & upper part of the embryo, but it now begins to decrease in quantity. This may be due in part to the fact that part of it becomes digested & built up into the tissue of the embryo & in part to its extension into the legs

A cross section of an embryo at a stage a little older than VI, ~~to~~ in a plane of a pair of limbs, is shown in figure 27. The ventral ganglia have increased enormously in size & have now a large amount of 'punct-substance'.

The middle of the section lies the mid gut with its contained yolk which has decreased very much as compared with preceding stages.

In figure 28 is drawn a section of another embryo, and at about the same stage as the last, but cuts the embryo between a pair of legs. Above the large ganglion is seen the digestive tract which is completely separated from the body wall by a series of sinus coels. The appearance of there, lying in the middle line is the heart, H.

At the sides of the midgut appear two well marked cavities & a third between the nerve ganglion the outer wall. Also below there are two or more spaces but these latter & perhaps some of the others are artefacts.
The mesenteron is covered on its outer side by a distinct layer of mesoblast cells. Cross section of some of the legs, lying below the body, are also shown in the figure.
Between stage VI & stage VII - VIII there is a considerable gap. During this period the embryo has lengthened & the fourth pair of walking legs has appeared. The rudimentary abdomen has been pushed up dorsally & the proctodaeum invaginated until at stage VII it has opened into the mesenteron

the eyes are now seen but at stage VI. They are seen in sections as four thickenings of the epiblast above the brain. In stage VII - VIII we find by sections that the yolk has almost completely disappeared from the digestive tract. Cross sections also show the large nerve ganglia, the mid-gut with its diverticula, & on the dorsal part of the mid gut is the tubular heart, running from the first walking leg to the third.

Figure 16 is from a cross section through the posterior part of the embryo & cuts the mid-gut at its juncture with the proctodaeum. Below the digestive tract D is a pair of small ganglia, $V^7$. which are the ganglia of the rudimentary abdomen. On account of the shifting of the abdomen to the dorsal side, these ganglia

have been carried above the last ventral ganglia which are shown at $V^6$.
But this is not all for this sixth pair of ganglia has itself been affected by the shifting of the abdomen & in turn lies above & back of the fifth pair of ganglia. In the sixth pair of ganglia, as shown in the figure, we have evident traces of the ventral organs. In the upper part of the section & on each side of the middle line are the diverticula of the fourth pair of walking legs. A few scattered mesoderm cells appear in the cavity of the body.
The embryo must leave the male at about this time for I have never found older embryos attached & only exceptionally ones so old as those last figured

Comparisons. Comparing the embryology of the two types represented by Phoxichilidium & Pallene we find that most of the changes of the latter may be considered by considering it an abbreviation of the type represented by Phoxichilidium.

An exact comparison of the segmentation of the two forms would be of interest but in order that such a comparison should be of value the exact orientation of the segmentation planes would be essential & such observations are wanting.

It would seem à priori most probable that the first planes in each must correspond & that the unequal segmentation of the egg of Pallene has been caused by the greater accumulation of yolk in that part of the egg which corresponds to the macromeres.

It is also probable the [illegible]

— the micromeres — correspond either to the anterior or to the ventral part of the embryo. Which of these is correct it is difficult to say. The embryo differentiates earlier in what corresponds to the anterior region of the adult than over the whole ventral surface, which suggests that the smaller cells may have adapted themselves to this early differentiation; but it seems equally possible that this differentiation may be due to Phylogenetic laws in this particular case rather than to any mechanical connection with the micromere differentiation. So that for the present the question must remain unsettled until by actual experiment (which would not be difficult) the orientation of the segmentation planes be determined.

There is an observation on the segmentation of the egg of Pallene brevirostris by Hoek

was mentioned in the previous description of segmentation of Pallene empusa.
He says "Le fractionnement commence par le fractionnement du noyau, et seulement après que quatre noyau sont formés, une premier fractionnement devise l'oeuf en une partie plus grand et une autre beaucoup plus petite.
Chaque partie contient deux noyaux qui dans le plus petit segment sont plus rapprochés l'une de l'autre que dans l'autre segment."
I cannot believe this a correct observation in the light of what I have observed over & over again in Pallene empusa.
There is a stage which corresponds exactly with the description but the egg shell has previously divided into two with a single nucleus in each segment & subsequently

each of these nuclei divides into two just before the segment itself divides & at the same time the first furrow becomes more distinct again as the segments round off to form the second furrow & this seems to be the stage which Hoek has described as the first segmentation.
Nor does it seem probable that the differences of our observations are due to their having been made on different species for in each case the egg is approximately the same size.
The changes which take place in the formation of the endoderm of Pallene may also I believe be reffered to the simpler changes of Phoxichilidium &c and furnish in this respect an excellent basis for further comparison with other forms having much yolk present. In Phoxichilidium

pyramidal segments divide into an outer & an inner cell while in Pallene the nuclei alone divide & although delamination is still multipolar it is not synchronous over the egg.
A further comparison of the mesenteron I am unable to give owing to lack of complete observations of the changes of Phoxichilidium. In both types the oesophagus invaginates with a triangular lumen & in each the proctodaeum forms quite late in development.
The few observations I have made on the ventral organs of Tanystylum leave no doubt that it is the same structure as in Pallene. Prof. Sedgwick has described in Peripatus paired ventral organs corresponding in number & position with the pairs of ventral ganglia.

Comparing figure 21 Plate 11 with his figure for the ventral organs of the jaws of Peripatus (Studies. Morph. Lab. Camb. Vol IV. Pt I. Plate 10. fig. 4.) a striking similarity is seen & in addition to this he says in his account of the ventral organs that they are slightly invaginated from the surface.

Whether these structures are in any way related it is impossible to say but it is worth while to call attention to the close similarity both in position & structure between these organs in the two groups.

In comparison of the appendages & their order of developement is of interest.

Prof Dohrn has most carefully & fully worked out the transformations of the larval forms, & through his skill we have a very thorough knowledge of the transformation of the embryo.

According to his account the six legged larvae of the Pycnogonids with the Pantopod-development passes into the adult condition by the body elongating behind the last pair of appendages & the walking legs appearing from before backwards, in much the same way as Prof Claus believes the typical-nauplius to pass into the adult

During the growth of the walking legs the second pair of appendages of the Pantopod-larva has increased a little in size but the third pair loses its spines & the whole appendage becomes a simple prolongation of the embryo. At a later stage, when the larva has increased in size this third pair grows out again to form the ovigerous legs

In Pallene we have seen that the second

fifth sixth pairs of appendages appear simultaneously in the embryo. The seventh comes in very much later & the third after the seventh. The second did not appear at all in the ontogeny so that in the young Pallene the only appendages in the young embryo that correspond to those of the Pantopod-larva are those of the first pair.

The developement of Pallene has become so much abbreviated that there is only a trace of the three Pantopod-larva found in its ontogeny.

# Phylogeny.

There is a general agreement that the Pycnogonids are to be placed within the large group of Arthropoda, but after this there is the greatest divergence of opinion as to which group of Arthropods they are most nearly allied.

In general there are two prominent categories to which all or nearly all of these theories may be referred. One lot of workers believe in a Crustacean relationship, & another lot placed the Pycnogonids amongst the Arachnids. It is needless to give here the reasons assigned for these opinions as Prof. Dohrn has given in his monograph of the Pantopoda of the Gulf of Naples a most complete & exhaustive bibliography of the literature.

The two most important views which we have at present are those of Dohrn & of Hoek, but as the latter agrees with much, that the former has given, we may consider the two together.

Prof Dohrn's earlier view of the relationship of the Pantopod-larva to the Nauplius he has completely given up in his more recent papers.

In an appendix to his paper in the Archives de Zoologie Experimentale Dr. Hoek gives a summary of Dohrn's recent theory as to the Phylogenetic position of the Pycnogonids; & has at the same time contrasted his own views with Dohrn's so that a translation of a part of this review will best bring out the resemblances & differences of their opinions.

"For the Crustacea Dohrn rejects the Nauplius Theory (of Fritz Muller & Claus) & adopts that of Haeckel, who believes the Crustacea to have descended from parents which had the form of Phyllopods, just as these Phyllopods have in turn descended from Annelids. From these same Annelids, according to Dohrn, the Pycnogonids have come down. The number of their segments was originally more numerous than we now see them, the presence of a pair of rudimentary ganglia in connection with the last pair of ventral ganglia allows us to add an eighth pair of appendages, & together with the first all of these appendages were originally homotypes, .... the received diverticula from the intestine ... & each appendage enclosed within itself a reproductive organ

with a special genital opening.
(The so-called cretory organs of the palpus & of the ovigerous legs are the rudimentary sexual organs of these appendages). The appendages were much shorter than we now see them, the heart showed many openings &c &c: The supposed ancestor that Dohrn reconstructs might be very well compared to an Annelid.
We also notice that Dohrn persists in his opinion, published in his work of 1879, that the Pycnogonids have a parentage neither with the Arachnids nor with the Crustacea (they have developed by the side of the last & altogether independently). In this I am in accordance with Dohrn.
I was struck in the first place by the

"very general presence in the Pycnogonids of a characteristic larval form (the Protonymphon) & its presence suggested to me the idea of their descent from an ancestor resembling somewhat a larva which took its place by the side of the hypothetical ancestor of the Crustacea - the Nauplius - & this by the side of a third (the ancestor of the Annelids); & that all three groups would have descended from a common ancestor. I had tried to obtain in this way an explanation of the affinities of the three groups of animals (Annelids, Pycnogonids, Crustacea).

Dohrn on the contrary took into account the larval forms but constructed a Phylogeny comparing together those animals having a considerable number of segments. It is true I do not wish

"to deny that such a method of looking at it have not just as good a basis of reason, only it appears to me at present that it can be defended just as little & certainly no better than the larval theory.

No one affirms that the intestinal diverticula which now in Phoxichilus & hymphon penetrate into the proboscis were originally [ancestrally] in the palps & ovigerous legs. The homology of the glandular organs of appendages II & III with parts of the sexual organs is not based on any observation ---- . But since I believe there are certain things which lessen Dohrn's arguments in favor of the Annelid theory, I believe that at bottom and the contents of pages 82 – 115 of his work confirms this opinion – the

"ideas of this author & of mine upon the Phylogeny as well for the Crustacea as for the Pycnogonids are not very different. At first I saw only the weak side of Dohrns theory that he does not give any explanation of the almost universal presence in the ontogeny of these animals of a characteristic larval form (the larval Protonymphon which for myself, is a true primary larva in the sense of Balfour. So that I cannot adopt a theory which causes to arise a form of Arthropods with many segments from an Annelid with the same number of appendages; but such is not the opinion of Dohrn as clearly expressed in the following paragraph.

"Thus the larva of the greater part of the Pycnogonids may be regarded, with a grain of salt, as a form much like the ancestor;

" but if on the other hand the absence of an anal opening, the pincers of the first pair of appendages, the long claws with their accessory spines, the structure of the proboscis with its triturating apparatus & its ganglia, & the form of the cutaneous glands with their integumentary hairs can only be considered as having been acquired in a much later stage & transmitted to larval life where they are found at present; but what remains in the larva that we may regard in reality as inherited from its original condition. Nothing but the nervous system i.e. the the brain & ganglia, an intestine, three pairs of appendages of a form modified according to circumstances & two eyes! But there are attributes which we finds equally in the larva of Annelids

"with three segments." And of these we take into consideration that at one time the body of the Pycnogonids, as we believe, showed a great uniformity in the segments (& the generative organs from this) that on the one hand there was a concentration & a differentiation & on the other hand a reduction in number of segments, these two conclusions lead us to admit a direct descent of the Pycnogonids from ancestral annelid-forms which were homonomously segmented

Then the larva of the Pantopods came from a larval form with pantopod-characters added on, but at the same time a larva which never had an independent & mature existence."

Whatever Hoek's position may be with respect to the Pantopod-larva he agrees

with Dohrn in the most important part of the Fallen's theory that the Pycnogonids have come down from the Annelids independently of the other groups of Arthropods. In examining the preceding account we may take it up, for the sake of clearness in two parts, the first pertaining to the ancestry of the adults leaving the larval form out of account & the second part where the meaning of the larval form will be considered.

I believe that if the account I have given of the early stages of development be even approximately correct there is little or no ground for a comparison between Crustacea & Pycnogonids certainly not with any existing forms.

The multipolar delamination of the

endosteron in the Pycnogonids has no homologue among the Crustacea nor is there any special similarity in the formation of the organs. There seems to be no trace of gastrulation in the ontogeny of the group. And if we have reason for rejecting a relationship between the Pantopod-larva & the Nauplius — and I believe with Dohrn that we have — there remains nothing in common to the ontogeny of the two groups.

Nor are there any special affinities between the Insects & Sea-Spiders, but there is one striking similarity between the latter & Peripatus, which I have already spoken of; but an isolated fact of this kind gives little ground for further comparisons.

The ventral organs in the two groups present a striking agreement but there is no proof forthcoming as to a real homology of the structures
The process of the formation of the endoderm described by Heider & by Wheeler in Insects shows a certain resemblance to multipolar delamination, but if it be such, it is in a more complicated form than shown by the Pycnogonids. With these two exceptions there seems to be nothing else in common in the ontogeny.
We are then left to decide between an independent origin for the Pycnogonids or a relationship with the Arachnids.
Prof Dohrn has ably maintained the first theory & the preceding translation gave the conclusion he had reached.

Dr Hoek however, as we have seen, holds this opinion although not agreeing as to details with Prof Dohrn. On the other hand a study of the early stages of the embryology has brought to light certain facts, which for me, point decidedly toward a community of descent between Arachnids & Pycnogonids. The latter show undoubted traces of degeneration & we cannot derive them from any existing animals. But I believe the Pycnogonids & the Arachnids have come down along the same line or in other words have had ancestors in common long after those ancestors came from Annelid-like forefathers.

The reasons for such a belief are as follows

1st. The Pycnogonids form the endoderm by a process of multipolar delamination which is shown in its simplest form in Phoxichilidium & Tanystylum & in a more modified condition in Pallene. In no other group of the Triploblastica do we find a similar phenomenon except in the Arachnids. The description of the embryology of Chelifer which Metchnikoff has given shows this process, or something quite analogous, to take place in it. The segmentation is holoblastic & at a later stage the large cells containing yolk divide into an outer more protoplasmic layer of cells & the inner cells which are very granular. The outer form the ectoblast & most probably the inner, judging from the figures

form the entoblast.

In the Spiders the process is not so well marked but if the conception which Balfour had of the formation of the yolk-nuclei be true, then we may make a direct comparison between the two groups.

He says " It appears to me probable that at the time when the superficial layer of protoplasm is segmented off from the yolk below the nuclei undergo division so that a nucleus with surrounding protoplasm is left with each yolk column"

This description for the Spiders may be substituted word for word for the process of delamination of Pallene.

2nd. The first traces of the entoderm to appear in Pallene is a round opaque area at the spot where the

stomodaeum invaginates.
In Schimkewitsch's recent account for the Spiders he shows that the primitive cumulus in them is the place where the stomodaeum invaginates. This is also true for Pallene but here the stomodaeum invaginates quite early, or perhaps simultaneously with the early formation of mesoblast at this place. Further Schimkewitsch has called attention to the fact that the stomodaeum of Spiders in its earliest developement is a triangular invagination & he compares it directly with the triangular invagination of the oesophagus of the Pycnogonids
3rd. The early formation of body cavity surrounded by mesoblast in the legs of Spiders has an exact parallel in

Pallene & Anoplodactylus. Yet however tempting such a comparison may be in this connection it must be admitted I have not conclusively proved this to be true for the Pycnogonids but only exceedingly probable

14th. In both Arachnids & Pycnogonids we have well marked diverticula from the mid-gut into the legs.

In the Pycnogonids these go into the chelicerae & the four pairs of walking legs & the same holds for the spiders but from a comparison of the appendages of the two groups we must suppose that the third pair of Pycnogonids appendages to have lost their diverticula & the last appendages either to have acquired diverticula, or more probably inherited them together with the appendage.

In Chelifer the diverticula appear very early in development & contain some of the yolk from the mid-gut. This is shown very distinctly in Metchnikoff's figures for Chelifer & in this respect the embryo resembles closely the embryos of Pycnogonids.

5th In both Arachnids & Pycnogonids the first pair of appendages are chelate. This in itself would draw attention to the similarities of the two groups but we know further that in both groups this first pair of chelate appendages is innervated from the brain. These facts were considered by Balfour sufficiently important to indicate alone a relationship between the groups. He says. "The presence of chelate appendages

innervated in the adult by the supra oesophageal ganglia rather points to a common Phylum for the Pycnogonida & Arachnida, though as shown above all the appendages in the embryos of true Arachnida are innervated by post-oral ganglia."

I have not been able to find any post-oral ganglia for Pallene but the first pair of appendages arises on the sides of the stomodaeum & later move forward. In this respect it compares closely with the Spider & the early innervation of this pair from the brain itself may be regarded as a more abbreviated condition than what was seen (by Balfour) in the Spiders. Metschnikoff's figures for Chelifer show the first pair of appendages to arise

above & on each side of the proboscis-like upper lip.

If future work verifies Metchnikoff's suggestion that this proboscis (rüsselförmige, provisorische Oberlippe) is homologous (entirely or in part) to the proboscis of the Pycnogonids — as his figure might indicate — then does the whole developement of Chelifer show remarkably close resemblances to the Pycnogonids.

6th. The fourth pair of ambulatory legs — the seventh pair of appendages has been a stumbling block in the way of those who have compared Pycnogonid with Arachnid. Semper & Schimkewitsch have attempted to solve the difficulty by assuming that the third pair of appendages of the Pycnogonids — the ovigerous legs — are new structures

have called the four pairs of walking legs homologous in the two groups.
Prof Dohrn has shown the impossibility of dropping out in the current, the ovigerous legs & has shown that this pair of appendages are homonomous with the others.
The two pairs of Sense Organs in the larval anterior ganglion we have seen point unmistakeably to the same conclusion, & give the final proof, if such were really necessary.
We are lead then to a comparison of the appendages of the two groups beginning with the chelicerae & going back pair for pair which leaves one pair over for the Pycnogonids. Any comparison between the two groups must take into account this extra pair of legs. Balfour has suggested that this last segment

appendages to represent the first abdominal segment of the Arachnids.
The third pair of appendages of the Pycnogonids have assumed a special function & at this time we might suppose that an additional pair to have been added on from the abdominal segments, we also know that the embryos of Spiders have rudimentary appendages on the abdomen & as we have assumed the Pycnogonids to have come from the latter group not recently but remotely when their appendages may have been larger or even functional we have some ground for a belief of such an origin of the last segment.
There is another fact which may be of importance in this connection
but only is the search pair of ganglia carri

dorsalwards by the abdomen but at the same time the sixth pair of ganglia also is carried dorsalwards above the fifth pair, from which the connecting nerve fibres pass upwards to the sixth. At the present time it is impossible to determine whether this is due to a mechanical adjustment between the shifted abdomen & the last pair of thoracic ganglia or whether the sixth pair, belonging properly to the abdomen has taken part in the general shifting of that structure *

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* If we assume with Hatchek a common descent for all Arthropods & that in the Insects we have reversal of the anterior segments, about the mouth, suppressed, we might assume that the Spiders have lost a third pair of appendages & the Pycnogonids retained it & in this way bring into line the other appendages of the groups.

There are certain objections against this comparison which I have attempted & if they do not directly oppose yet do not support the hypothesis.

First & most important is the uncertainty of brain invaginations in Pycnogonids. These seem to be present in all the Arachnids & easily seen in the developement of the embryo. In the Pycnogonids I have not been able to find such invaginations. We have seen in figure that the groove might possibly bear such an interpretation but even if this were true we would expect to find a much more pronounced involution but this does not seem to be the case. Again the Ventral Organs which have been compared with those of Peripatus lend no support to the hypothesis.

It is possible that the Pycnogonids have come from the Arachnids at a time when these latter have had such organs in common with the ancestors of the Insects & that they have been fully retained in the Pycnogonids

Lastly the openings of the reproductive organs. Typically the ovaries & testes of the Sea-Spiders are a pair of organs united posteriorly by a cross commissure They extend into the walking legs & open on the second joint of these. There are many exceptions to this but they are regarded as secondary.

The openings on the legs have no homologue in the Arachnids nor does it furnish any ground for comparison with other Arthropods. But if we assume the group to have come directly from the

Annelids we have no better ground here for a comparison. We are greatly in need of observations on the developement of the sexual openings & until we get such the question must remain an open one.

It seems not improbable however that the openings may be secondary & connected in some way with the secondary presence of reproductive organs in the appendages.

I hope to have shown, that these three objections are of negative value, at any rate so long as the present uncertainty surrounds them; & that we have sufficient grounds for a comparison in the early stages of developement, & in some of the important adult structures of the two groups.

The Pantopod-larva.

There is a general resemblance between the Nauplius of the Crustacea & the larva of the Pycnogonids, but the differences become greater & greater the more closely we examine the two forms. In each the body contains three pairs of appendages but there in the Nauplius show biramous structures while none of the Pantopod-larval appendages show such structures. Moreover the first pair of appendages of the Pantopod larva is chelate & innervated from the brain. Other characteristics of the larva are the well marked proboscis with its triangular oesophagus, the mid-gut sending out prolongations into some of the appendages & the absence of any anal opening.

Have we then any basis for the assumption that this Pantopod-larva is a modified Trochophore of the Annelid ancestors? The problem is very similar to that of a supposed relationship between the Amphiura & the Trochophore, & in both cases an answer exceeding difficult to give. Prof Dohrn believes that the Pantopod-larva is to be regarded as a Trochophore with the Pycnogonid characteristics reflected onto it. Prof Lang believes in a similar process for the Amphiura. Without discussing the latter let us confine our attention to the possibilities of the Pantopod larva.

What characters have been reflected on Dohrns theory & what remains after these are removed? Prof Dohrn

has given us the answer.

" ..... The absence of an anal opening, the pincers of the first pair of appendages, the long claws with the accessory spine, the structure of the proboscis with its triturating-apparatus & its ganglia, the form of the segmentary glands & their characteristic hairs, can only be considered as having been acquired in a much later stage, & transmitted to larval life."

That is to say that almost every characteristic of the larva has been handed back from the adult! And what remains?

"Nothing but the nervous system — an intestine, three pairs of appendages & two eyes." "But these are the attributes which one finds equally in the larva of Annelids"! There is one other part

which has been left out of account, viz, the presence of an anus in the Trochophore. How can we account for its absence on the above hypothesis when we know the Pantopod-larva to be a free ~~swimming~~ larval-form. And unless some special reason for such a loss can be imagined the very basis of the comparison between Pantopod-larva & Trochophore is gone! What we have done in the above process of subtraction is to have removed the most striking structures of the adult from the larva & have left — not a Trochophore but only the framework of the Pycnogonid.

For two main reasons I am unable to believe in the Phylogeny given by Dohrn or by Haeckel. First because

it seems to me there are facts derived from the early stages of development which point unmistakably to a relationship between Pycnogonids & Arachnids.

And in the second place I cannot believe any actual homology to exist between the Pantopod-larva & the Trochophore, nor any fair reason to assume that the characteristics of the Pycnogonids have been reflected onto a Trochophore.

If then we start with the assumption that there is a relationship between the Sea-Spiders & Arachnids we may examine into the meaning of the larval form as a corollary to such a position.

I have stated that the Pycnogonids are degenerate & probably not derivable directly from

any existing group. If so how far down in the ancestral tree of the Arachnids have they arisen. The very great differences in the adult structure of the groups indicates no very recent origin but possibly they came in at a time when the Arachnids had the first pair of appendages chelate & there were innervated from the supraoesophageal ganglion; & had coeca from the digestive tract into most or all of the appendages. After the divergence of the Pycnogonids, as a group from the general phylum of the Arachnids the Pantopod-larva may degenerate.

The Pycnogonids have adapted themselves to a very special habitat, so that there must be very great advantages for distribution & intercrossing in a free-

swimming independent larval form
And in general what we may suppose to
have happened was a decrease in the
size & an increase in the number of eggs,
with the resulting early developement
of the free larva that we find to-day.
This larva represents the more anterior
segments of the adult viz, that part
containing the proboscis, the oesophagus
the eyes, the chelae, & two post-oral
appendages. Behind this is an undeve-
loped part which slowly grows in length
as the animal increases in size.
The arms belongs to the last segment
& does not appear until that segment
is wholly or in part developed.
If the Arachnids have come from Annelid
ancestors with many segments we have a clue
to the slight resemblance between the Pantopod

& the Trochophore. The former represents the most anterior segments of the adult Sea-Spiders & therefore to some extent the anterior segments of the Annelids or of the Trochophore. But at no time in the ontogeny of the Pycnogonids have Trochophore & Pantopod-larval characteristics existed separately as Dohrn believes.
Such seems to me the more probable view of the meaning of the Pantopod-larva. This belief has grown out of my work on the embryology of the group & whether future work supports or disproves such an hypothesis it is hoped it may be useful if only as furnishing another point of view for looking at the Phylogeny of the Pycnogonids, or may lead to a more complete study of the embryology of the group

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# Reference Letters.
(for plates.)

B = Brain.
D = Mid-gut, mesenteron.
D' D'' D''' D'''' oc = Diverticula of Mid-gut.
E = Ectoblast.
N = Entoblast.
M = Mesoblast
P = Periphery of Blastoderm.
S = Schizocoeles
V' -7 = Ventral Ganglia 1-7
H = Heart
L = Legs
O = Opening Ventral Organs
C = Central Cavity of Segmenting Egg.

# Description of Plates.

## Plate I

Fig 1. Section of segmented egg & membranes of Pallene empusa.

Fig 2. Section of another egg of Pallene at same stage to show central cavity C.

Fig 3. Section through upper pole of egg of Pallene. First formation of Blastoderm

Fig 4. Section through upper pole of egg of Pallene. Later stage than last. Inner cells - Entoblast - are present.

Fig 5. Section through egg of Pallene. Later stage than last. Cap of cells - blastoderm - covers more of egg than in last.

Fig 6. Section through periphery of blastoderm at P of figure 5.

Plate 1. (continued)

Fig 7. Section in same region as last

Fig 8. Section of segmenting egg of Tamystylum orbiculare to show pyramidal shape of cells.

Fig 9. Section of egg of Tamystylum, to show process of multipolar delamination

Fig 10. Same, with delaminated Entoblast

Fig 11. Section of segmenting egg of Phoxichilidium maxillare.

Fig 12. Same, to show degeneration of endoderm.

Fig 13. Cross-section of the Pantopod-larva of Tamystylum orbiculare.

Fig 14. Circumoesophageal ring of same

Fig 15. Eyes of same.

Fig 16 Ventral Organs of same
Early stage of third pair of ganglia.

# Plate II

## Section of Pallene empusa.

Fig 17. Longitudinal section through stomodaeum of young embryo. First origin of Mesoblast at M

Fig 18. Cross-section through stomodaeum of older stage. See line 18. Fig 1. Plate IV

Fig 19. Section anterior to last. See line 19. Fig 1 Plate IV

Fig 20 Section anterior to figure 19 See line 20. Fig 1 Plate IV

Fig 21 Cross section of Ventral Organ. See line 21. Fig 1. Plate IV

Fig 22 Cross section of Ventral Organs at stage III

Fig 23. Cross section of Ventral Organs at stage V

Fig 24 Cross section of Ventral Organs at stage VI

Plate II (continued)

Fig 25. Cross-section of embryo at Stage III

Fig 26. Cross-section through brain & second pair ventral ganglia of Stage III

Fig 27. Cross-section of embryo in the plane of a pair of legs. About Stage VI.

Fig 28. Cross-section of embryo in the plane between a pair of walking legs About Stage VI

Fig 28 Cross section through the rudimentary abdomen & the body of an embryo Stage VII — VIII

# Plate III.

A – J. Pallene empusa:

a – c. Phoxichilidium maxillare.

d – f. Pycnogonum orbiculare.

Fig A. Segmenting egg, side view, 2-celled stage.

Fig B. " ", seen from above, 4-celled stage.

Fig C. " " seen from above, 8-celled stage.

Fig D. " " seen from below 8 celled stage.

Fig E. " " side-view 16 celled stage.

Fig F " " Surface view of micromeres; 16 celled stage.

Fig G " " side view 16 macromeres, 8 micromeres.

Plate III (continued)

Fig H. Segmenting egg. side view.
24 macromeres
16 micromeres

Fig J Segmented egg. Lower Pole
Base of pyramidal cells
show at surface.

Fig. a. Phoxichilidium 2-celled stage
Fig b. " 4- " "
Fig c. " 8 " "

Fig d. Tanystylum orbiculare 2-celled stage
Fig e. " " 4- " "
Fig f. " " 32(?) " "

# Plate IV

I – VIII Pallene

IX Tanystylum.

Fig I. Surface view of young embryo, to show anterior region.

Fig II Surface view of ventral region of same.

Fig III Ventral view of embryo with four pairs ventral ganglia: First & second separate

Fig IV Dorsal view of embryo about same age (a little older perhaps) as last.

Fig V Ventral view of embryo. First & second ventral ganglia have fused.

Fig VI Side view of embryo Showing rudimentary abdomen behind as a continuation of the body & in same plane as the body

Plate IV (continued)

Fig VII Ventral view of embryo at the age when it leaves the parent. Fourth pair of walking legs seen behind. Third pair of appendages beginning just in front of first pair of walking legs.

Fig VIII Dorsal view of last to show brain & four eye spots.
In both VII & VIII only the proximal ends of the legs are shown.

Fig IX The Pantopod larva (Protonymphon of Hoek) of Tanystylum orbiculare.

# Life

Thomas Hunt Morgan was born Sept 25th 1866. Preliminary education received in Public & Private Schools in Maryland. In '80 entered the Preparatory School of the State College of Kentucky; in the Autumn '82 entered the College & graduated in the Spring of '86. Entered Johns Hopkins University in the Autumn of '86. The Summer of '86 was spent at the Boston Marine Laboratory at Annisquam Mass: the Summer of '87 at the Harvard School of Botany: of '88 at Beaufort, N. C., & at the U. S. Fish Commission Laboratory at Wood Holl, Mass; of '89 again at the last place.

The subjects offered for the degree of Doctor of Philosophy were Animal Morphology, Animal Physiology & Histology, & Morphological Botany.

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